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Taxonomy of subgenus *Temnoclemmys* Bergounioux, 1958 (Testudines: Geoemydidae: Ptychogasterinae) based on new material from the Vallès-Penedès Basin (NE Iberian Peninsula)



Taxonomie du sous-genre Temnoclemmys Bergounioux, 1958 (Testudines : Geoemydidae : Ptychogasterinae) sur la base du nouveau matériel du bassin de Vallès-Penedès (Nord-Est de la péninsule Ibérique)

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ARTICLE INFO

Article history:

Received 9 July 2013

Accepted after revision 27 November 2013

Available online 18 February 2014

Handled by Lars Van den Hoek Ostende

Keywords:

Ptychogaster (Temnoclemmys) batalleri

Ptychogasterines

"Ptychogasterids"

Fossil turtles

Miocene

Spain

Mots clés :

Ptychogaster (Temnoclemmys) batalleri

Ptychogasterines

« Ptychogasteridés »

Tortues fossiles

Miocène

Espagne

ABSTRACT

The taxonomy of the freshwater turtle subgenus *Ptychogaster (Temnoclemmys)* (Testudines, Geoemydidae, Ptychogasterinae) is revised based on new and previously-published material from the Vallès-Penedès Basin (NE Iberian Peninsula). Additional remains of subgenus *Ptychogaster*, first reported from this basin, are also described. Although the oldest remains of *Temnoclemmys* are left unassigned, most of the available remains are attributed to its type species, *Ptychogaster (Temnoclemmys) batalleri*, originally described from the Late Miocene (MN9 and MN10) of this basin. The new material expands the chronostratigraphic range of *P. batalleri* in the Vallès-Penedès Basin back to the MN7+8 and shows that "*Testudo celonica*" is its junior synonym. Emended diagnoses for *Ptychogaster* and *Temnoclemmys* are also provided.

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R É S U M É

La taxonomie du sous-genre de tortue d'eau douce *Ptychogaster (Temnoclemmys)* (Testudines, Geoemydidae, Ptychogasterinae) est révisée sur la base du matériel nouveau et déjà publié provenant du bassin de Vallès-Penedès (Nord-Est de la péninsule Ibérique). Des restes additionnels du sous-genre *Ptychogaster*, signalé pour la première fois dans ce bassin, sont également décrits. Bien que les restes les plus anciens de *Temnoclemmys* ne soient pas assignés, la plupart des restes disponibles sont attribués à son espèce type, *Ptychogaster*

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(*Temnoclemmys*) *batalleri*, décrite à l'origine dans le Miocène supérieur (MN9 et MN10) de ce bassin. Le nouveau matériel élargit le cadre chronostratigraphique de *P. batalleri* dans le bassin de Vallès-Penedès à MN7 + 8 et montre que « *Testudo* » *celonica* est son synonyme plus récent. Des diagnoses émendées sont également fournies pour *Ptychogaster* et *Temnoclemmys*.

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1. Introduction

The family Geoemydidae (Testudines, Testudinoidea) constitutes a diverse and widely-distributed group of freshwater turtles, with 69 extant species of world-wide distribution except for Australia and Antarctica (Marmi and Luján, 2012; Van Dijk et al., 2012). Fossil geoemydids are frequently recorded from Tertiary deposits of Europe, and among them, an extinct 'ptychogasterid' group—including *Ptychogaster* Pomel, 1847 and closely-allied genera—is recognized by several authors (Claude, 2006; Hervet, 2003, 2004a, 2006; Miklas-Tempfer, 2003). This group originated in the Eocene of Europe (Lapparent de Broin, 2001; Murelaga et al., 2002), and some of its most characteristic features (such as the ptychogasterid spikes) are already present in its basal-most known members, whereas others appear in later taxa and are known to have independently evolved more than once in the “*Palaeochelys* s.l.–*Mauremys* group” (Hervet, 2003, 2004a, 2004b, 2006). The genus *Ptychogaster* is further characterized by plastral kinesis, which is known to have convergently evolved several times within the Testudinoidea (Claude, 2006). The inclusion within 'ptychogasterids' of non-kinetic extinct genera (e.g., Hervet, 2006) has been questioned by Claude (2006). In any case, similarities in plastral morphology indicate that *Ptychogaster* belongs to the Geoemydidae (Claude, 2006).

Although some authors have previously concluded that 'ptychogasterids' constitute a monophyletic clade diagnosable by several synapomorphies (Hervet, 2004a, 2006), more comprehensive phylogenetic analyses than those currently available (Hervet, 2006) would be required in order to adequately test whether 'ptychogasterids' actually constitute a monophyletic group within geoemydids, as well as to further decipher which are their closest extant relatives among the latter. Largely as a result of such phylogenetic uncertainties, the systematic status of 'ptychogasterids' is currently unclear. Various former authors (Lapparent de Broin, 2000, 2001; Murelaga et al., 2002) referred these taxa to the infrafamily Geoemydinei (within the family Testudinidae), which is currently recognized as a distinct family, Geoemydidae, within the Testudinoidea (Fritz and Havas, 2007). Hervet (2003, 2004a), in turn, referred to this group as 'Ptychogasteridae'—the quotation marks indicating that no taxonomic value was implied. Later, the same author (Hervet, 2006) employed for it the name “Ptychogasteridae De Stefano, 1903 (*sensu* Hervet, 2004a)”, but given that phylogenetic nomenclature was employed, no family rank was apparently implied. Here we provisionally distinguish the extinct group including *Ptychogaster* and closely-allied genera as a subfamily, i.e. Ptychogasterinae—as done by some previous authors (Luján et al., 2013a, 2013b; Miklas-Tempfer, 2003)—within

the geoemydids (Claude, 2006). Future cladistic analyses (outside the scope of this paper) would be required in order to investigate the monophyly of ptychogasterines as well as their relationships with other geoemydids.

Two subgenera are currently distinguished within *Ptychogaster* (Lapparent de Broin, 2001), the type genus of this subfamily: *Ptychogaster* (*Ptychogaster*) and *Ptychogaster* (*Temnoclemmys*) Bergounioux, 1958. The type species of the latter, *Ptychogaster* (*Temnoclemmys*) *batalleri* (Bergounioux, 1931), has a very complex taxonomic and nomenclatural history (with many junior subjective synonyms, see later). This species was originally described in the Vallès-Penedès Basin (NE Iberian Peninsula), but since Bergounioux's (1958) revision of Tertiary reptiles from Catalonia, no detailed revision of the ptychogasterine turtles from this basin has been performed. Here we report new ptychogasterine material from several Vallès-Penedès localities, and further revise its taxonomy on the basis of all available remains, including those already described from the historical collections (see Luján et al., 2013a, 2013b, for preliminary reports in abstract form). Emended diagnoses of the genus *Ptychogaster*, its two included subgenera, and the type species of *Temnoclemmys* are also provided.

2. Materials and methods

2.1. Abbreviations

Institutional abbreviations: ICP: Institut Català de Paleontologia Miquel Crusafont; Universitat Autònoma de Barcelona (Spain); IPS: acronym of the collections of the ICP; MGB: Museu de Geologia (Museu de Ciències Naturals de Barcelona, Spain); MGSB: Museu de Geologia del Seminari de Barcelona (Spain).

Locality abbreviations: ACM: local stratigraphic series of Abocador de Can Mata (els Hostalets de Pierola); BDA: Bassa de Decantació d'Aigües Pluvials (ACM sector); CC: Can Canals (El Papiol); CM: Can Mata unknown location (els Hostalets de Pierola); CR: Can Rabassa (Sant Celoni); EC: El Canyet (Castellbisbal); EDAR: Estació Depuradora d'Aigües Residuals Sabadell Riu-Ripoll (Sabadell); HP: Hostalets de Pierola indeterminate (els Hostalets de Pierola); HPI: Hostalets de Pierola Inferior (els Hostalets de Pierola); HPS: Hostalets de Pierola Superior (els Hostalets de Pierola); LT: La Tarumba (Viladecavalls); SMT: Sant Miquel del Taudell (Viladecavalls); TS: subsoil of Terrassa (Terrassa); VC: Viladecavalls unknown location (Viladecavalls).

2.2. Anatomical terminology

Anatomical terminology is after de Broin (1977).

3. Age and geological background

All the fossil remains reported in this paper come from the Vallès-Penedès Basin (Fig. 1) in NE Iberian Peninsula. This basin is a NNE-SSW-oriented, asymmetric half-graben limited by the Littoral and Pre-littoral Catalan Coastal Ranges, which was generated by the rifting of the NW Mediterranean region during the Neogene (Bartrina et al., 1992; Cabrera et al., 1991, 2004; de Gibert and Casanovas-Vilar, 2011; Roca and Guimerà, 1992). Besides some Early and Middle Miocene shallow marine and transitional sequences, most of the basin infill consists of distal-marginal alluvial fan sediments, with a rich fossil record of late Middle and Late Miocene terrestrial vertebrates (Agustí et al., 1985; Casanovas-Vilar et al., 2011a). On the basis of the previously-available data for this basin (Agustí et al., 1997; Casanovas-Vilar et al., 2011a, 2011b), the following correlations with Mammal Neogene (MN) units are available for the localities that have yielded *Ptychogaster* remains: CC and EC (MN4; Early Aragonian, Early Miocene); HPI (MN7+8; Late Aragonian, Middle to Late Miocene); HP (MN7+8 to MN9; Late Aragonian to Early Vallesian, Middle to Late Miocene); CM (late MN7+8 to MN9; Late Aragonian to Early Vallesian, Middle to Late Miocene); HPS (MN9; Early Vallesian, Late Miocene); EDAR24 (MN9; early Vallesian, late Miocene); CR (MN9–MN10; Early to Late Vallesian, Late Miocene); LT, SMT, VC and TS (MN10; Late Vallesian, Late Miocene). It should be taken into account that HP, HPI, HPS, CM and VC are not paleontological localities in a strict sense, but rather loosely-defined areas that mix material from different stratigraphic horizons that cover a relative long time interval (Alba et al., 2006, 2010, 2011). The exact stratigraphic position of the new material from ACM is not recorded, but its provenance from sector ACM/BDA, on the basis of biostratigraphic and magnetostratigraphic data for the whole ACM series (Alba et al., 2006, 2011; Casanovas-Vilar et al., 2011b; Moyà-Solà et al., 2009), indicates an early MN7+8 (Late Aragonian, Middle Miocene) age.

4. Systematic paleontology

Order: TESTUDINES Linnaeus, 1758
 Infraorder: CRYPTODIRA Cope, 1868
 Superfamily: TESTUDINOIDEA Batsch, 1788
 Family: GEOEMYDIDAE Theobald, 1868
 Subfamily: PTYCHOGASTERINAE De Stefano, 1903
 Genus *Ptychogaster* Pomel, 1847

Type species: *Ptychogaster emydoides* Pomel, 1847.

Included subgenera: *Ptychogaster* (*Ptychogaster*) Pomel, 1847; *Ptychogaster* (*Temnoclemmys*) Bergounioux, 1958.

Emended diagnosis: Small to medium-sized geoemydid characterized by the following features: long peripherals; loose coincidence between the pleurals and the peripherals at the posterior part of the shell; posteriorly narrow suprapygal 1; sulci between marginal 12 and vertebral 5 situated on pygal; reduced anal notch; somewhat

elongated internal ventral underlap of cervical; dorsal epiplastral lip long and narrow; entoplastron pyriform to rhomboid, longer than broad, and with rounded posterior margins; humeropectoral sulcus overlapping with the entoplastron, from about its midlength to three-quarters of the latter; wide dorsal overlap of the plastral scutes; narrow anterior edge of the anterior plastral lobe; vertebral 1 not completely covering the nuchal; irregular neural series formed mainly by octagonal and hexagonal plates with short sides in front; and nuchal longer than wide, markedly concave internally, and with a well-developed pair of internal thickenings. Further characterized by the following apomorphies: reduced axillary buttresses (approximately one-third of pleural 1 width); absent inguinal buttresses; completely ligamentous union between hypoplastron and peripherals; presence of a hinge between hyoplastron-hypoplastron; octagonal neural 2; well-developed pair of internal thickenings on the ventral surface of nuchal.

Differential diagnosis: *Ptychogaster* differs from other Geoemydidae by displaying a well-developed pair of internal thickenings on the nuchal plate. It differs from all other ptychogasterines (sensu Hervet, 2006) in the six apomorphic features mentioned above in the diagnosis. It further differs from all other ptychogasterines except “*Geoemyda*” *saxonica* Hummel, 1935 and *Clemmydopsis Boda*, 1927 in the position of sulci between marginal 12 and vertebral 5 on pygal—although this feature cannot be evaluated in *Geiselemys* Khosatzky and Młynarski, 1966. It also differs from other ptychogasterines except *Clemmydopsis* in the longer peripherals (sometimes with marked anterior expansions), the entoplastron longer than broad and with more rounded margins, and the markedly narrower anterior border of the plastral lobe. *Ptychogaster* also differs from *Hummelemys* Hervet, 2004b and *Merovemys* Hervet, 2006 in the loose coincidence between the pleurals and peripherals at the posterior portion of the shell; from *Merovemys* and *Clemmydopsis* in the posteriorly narrow suprapygal 1; from *Hummelemys* in the somewhat narrower and much longer dorsal epiplastral lip, the somewhat longer internal ventral underlap of the cervical, and the wider and more extensive dorsal overlap of the plastral scutes; from *Merovemys* in the larger overlap between the humeropectoral sulcus and the entoplastron, and in the presence of anal notch (albeit reduced); and from *Clemmydopsis*, in the less reduced axillary buttresses, less elongate nuchal (not longer than wide), the lack of fused costal and vertebral scutes, and in the fact that the posterior vertebrae are not wider than the costals.

Subgenus *Ptychogaster* Pomel, 1847

Other included species: *Ptychogaster* (*Ptychogaster*) *laurae* (Förster and Becker, 1888); *Ptychogaster* (*Ptychogaster*) *sansaniensis* (De Stefano, 1903); *Ptychogaster* (*Ptychogaster*) *grepiacensis* (Bergounioux, 1935); *Ptychogaster* (*Ptychogaster*) *ronheimensis* Groessens-Van Dyck and Schleich, 1985.

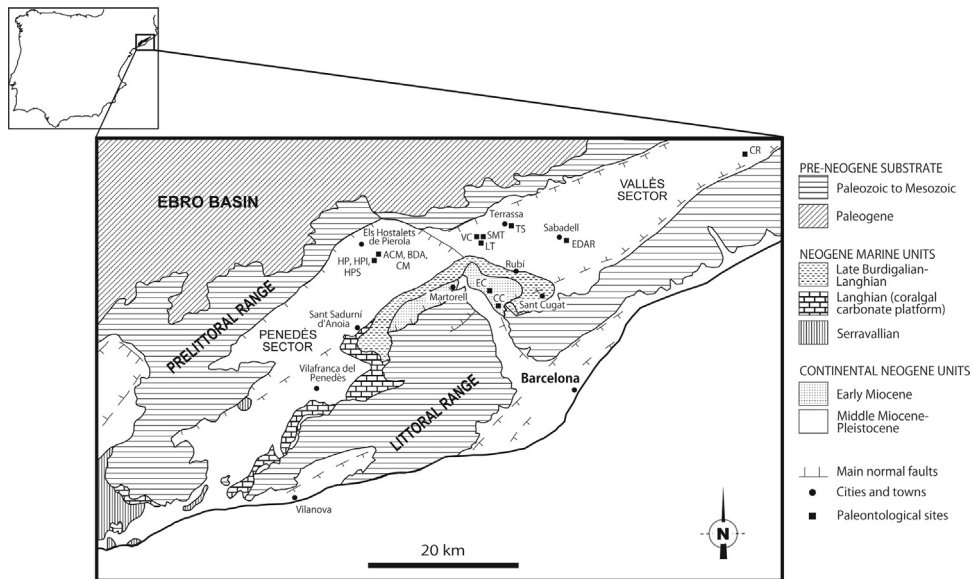


Fig. 1. Schematic geological map of the Vallès-Penedès Basin, showing the sites that have delivered remains of *Ptychogaster*. ACM: Abocador de Can Mata; CC: Can Canals; EC: El Canyet; CR: Can Rabassa; EDAR: Estació Depuradora d'Aigües Residuals Sabadell Riu-Ripoll; LT: La Tarumba; SMT: Sant Miquel del Taudell; TS: subsol of Terrassa; VC: Viladecavalls.

Fig. 1. Carte géologique schématique du bassin de Vallès-Penedès, montrant les sites qui ont livré des restes de *Ptychogaster*. ACM : Abocador de Can Mata ; CC : Can Canals ; EC : El Canyet ; CR : Can Rabassa ; EDAR : Estació Depuradora d'Aigües Residuals Sabadell Riu-Ripoll ; LT : La Tarumba ; SMT : Sant Miquel del Taudell ; TS : sous-sol de Terrassa ; VC : Viladecavalls.

Diagnosis: As for genus. See below for a differential diagnosis with subgenus *Temnoclemmys*.

Ptychogaster (*Ptychogaster*) sp.
(Figs. 2A–H, 3A–H)

Material: IPS64018 (Figs. 2A–B, 3A–B), partial right and left epiplastron (possibly also a little portion of entoplastron) from EC; IPS64019 (Figs. 2C–D, 3C–D), left partial peripheral 7 from CC; IPS64022 (Fig. 2E–F, 3E–F), right epiplastron from HPI; IPS64023 (Fig. 2G–H, 3G–H), partial nuchal from HP.

Stratigraphic range in the Vallès-Penedès Basin: MN4 (Early Miocene) to MN7 + 8–MN9 (Middle to Late Miocene).

Description of the new material: Based on the dimensions and structure of the peripheral plate and the epiplastron (in the material from EC) and the partial nuchal and right epiplastron (in the material from els Hostalets area), the shell would have been relatively large (> 20 cm). The dermal grooves and bony sutures are visible.

The peripheral 7 of IPS64019 (Figs. 2C–D, 3C–D), which is nearly complete, is approximately rectangular in shape. In internal view, it displays a rough elongated area for the cartilaginous union with the inguinal process. It hosts the sulcus between marginals 7–8 and the costo-marginal sulcus, which is situated close to the pleuro-peripheral suture.

Despite some fractures affecting the anterior edge of the right epiplastron just medial to the right edge of the epiplastral lip, the ptychogasterid spike seems to be present but small in IPS64018 (Figs. 2A–B, 3A–B); it is developed in posterior direction, slightly medially, although close to the gulohumeral sulcus, where it is poorly developed, not

protruding dorsally and weakly defined. The epiplastral dorsal lip is only partially preserved, but its shape was most likely subrectangular. Its dorsal surface is somewhat concave medially, slightly thickened and anteroposteriorly long, imperceptibly shortening in medial direction so that its posterior edge is only slightly concave. The remnants of the anterior edge indicate that it was clearly concave, but for preservational reasons it is not possible to assess the depth of the concavity. On the basis of the small preserved portion of the gular area, it is possible to state that this element was extremely short and triangular, with rounded lateral margins, and probably not covering the anterior portion of the entoplastron.

On the basis of the right epiplastron IPS64022 (Fig. 2E–F, 3E–F), it seems that the anterior plastral lobe was anteriorly truncated and slightly concave. The covering of the scutes on the dorsal surface of the epiplastron is well developed, resulting in an anteroposteriorly long epiplastral lip. The ptychogasterid spike is partially preserved. The area of the epiplastral lip posterior to the spike, and located medially to the gulohumeral sulcus, is roughly triangular and distinctly elongated, but not significantly protruding dorsally. The epiplastral dorsal lip of the isolated epiplastron is slightly wider than long. Its posterior edge is approximately straight and its dorsal surface is moderately concave medially. The gulars are proportionally long (covering the anterior portion of the entoplastron), triangular-shaped, with slightly rounded lateral margins. The dorsal overlap of the humeral scute on the epiplastron is well developed.

IPS64023 (Fig. 2G–H, 3G–H) is hexagonal, probably slightly wider than long and highly concave ventrally. The anterolateral edge is vaguely concave. In lateral view,



Fig. 2. (Color online). Shell remains of *Ptychogaster* (*P.*) sp. (A–H) and *P.* (*Temnoclemmys*) sp. (I–L) from the Vallès-Penedès Basin. A–B, IPS64018 from EC, in A, dorsal; B, ventral views. C–D, IPS64019 from CC, in C, dorsal; D, internal views. E–F, IPS64022 from HPI, in E, dorsal; F, ventral views. G–H, IPS64023 from HP, in G, dorsal; H, internal views. I–J, IPS64020 from CC, in I, dorsal; J, ventral views. K–L, IPS64021 from CC, in K, dorsal; L, internal views. **Fig. 2.** (Couleur en ligne). Restes de carapace de *Ptychogaster* (*P.*) sp. (A–H) et *P.* (*Temnoclemmys*) sp. (I–L) du bassin de Vallès-Penedès. A–B, IPS64018 de EC, en vues A, dorsale; B, ventrale. C–D, IPS64019 de CC, en vues C, dorsale; D, interne. E–F, IPS64022 de HPI, en vues E, dorsale; F, ventrale. G–H, IPS64023 de HP, en vues G, dorsale; H, interne. I–J, IPS64020 de CC, en vues I, dorsale; J, ventrale. K–L, IPS64021 de CC, en vues K, dorsale; L, interne.

the nuchal is faintly concave, and the posterior edge of the cervical corresponds to a change in slope. The cervical is very large, triangular, and posteriorly quite wider, with a concave posterior edge and convex lateral margins. The internal overlap of the cervical is long and well developed. The left marginal 1, which is partially present, was apparently rectangular and slightly longer than wide. The vertebral 1, which is partially preserved, does not completely cover the nuchal because it is fairly narrow anteriorly; the small preserved portion of the left lateral vertebral–costal sulcus is slightly concave, possibly indicating that the vertebral was lyre-shaped.

Subgenus *Temnoclemmys* Bergounioux, 1958

Type species: *Ptychogaster* (*Temnoclemmys*) *batalleri* (Bergounioux, 1931).

Other included species: *Ptychogaster* (*Temnoclemmys*) *cayluxensis* Lydekker, 1889; *Ptychogaster* (?*Temnoclemmys*) *francofurtanus* Reinach, 1900 (nomen dubium); *Ptychogaster* (*Temnoclemmys*) *bardenensis* Murelaga et al., 1999.

Emended diagnosis: The subgenus *Temnoclemmys* differs from *Ptychogaster* s.s. in the following features: smaller size (adult shell length around 10–16 cm vs. 20–30 cm); much shorter cervical both dorsally and internally (not preserved in *P. cayluxensis*); trapezoidal (instead of rounded) margin of the anterior lobe and more tapering posterior lobe of the plastron (the latter only preserved in the type species); thicker epiplastral lip (at least medially, close to the gular sulci and the ptychogasterid spikes); shorter peripherals 1–2 without marked anterior expansions (only preserved in the type species); and shorter nuchal (i.e., shorter than wide; only preserved in the type species). The two latter features cannot be ascertained for *P. (T.) bardenensis*.

Ptychogaster (*Temnoclemmys*) sp.

(Figs. 2I–L, 3I–L)

Material: Two shell fragments of the same individual from CC, including: IPS64020 (Figs. 2I–J, 3I–J), partial left epiplastron (a little portion of entoplastron is possibly

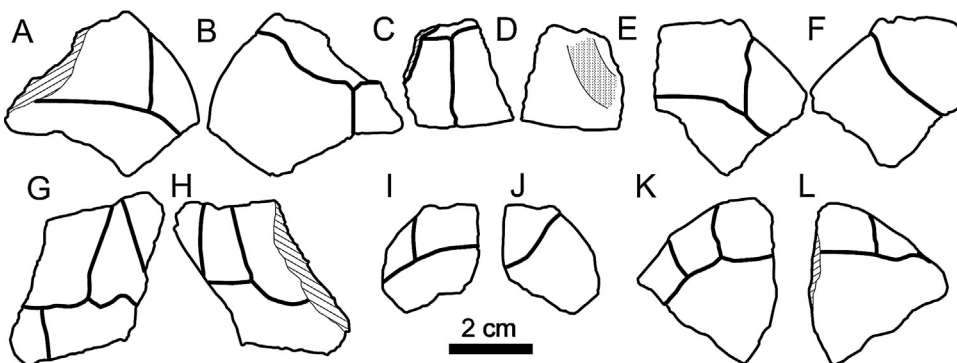


Fig. 3. Schematic drawings corresponding to the fossil remains depicted in Fig. 2. Thick lines correspond to scute sulci, dotted areas indicate ligamentous joints, and oblique lines denote missing portions or sediment.

Fig. 3. Dessins schématiques correspondant à des restes fossiles illustrés sur la Fig. 2. Les lignes épaisses correspondent aux écailles, les zones en pointillés indiquent des articulations ligamentaires, et les lignes obliques indiquent des portions manquantes ou du sédiment.

present); and IPS64021 (Figs. 2K–L, 3K–L), left peripherals 2–3.

Stratigraphic range in the Vallès-Penedès Basin: MN4 (Early Miocene).

Description of the new material: Based on the dimensions of the plates, the shell was small and thin. Most of the dermal grooves are visible, although the sutures are fairly obliterated.

The shape of the peripherals 2–3 IPS64021 (Fig. 2K–L, 3K–L) cannot be assessed with confidence. The sulci delimiting the marginals 2–4 are visible. Marginal 3, the only complete scute, is longer than wide. In internal view, the overlap of the marginals is moderately developed.

The epiplastron of IPS64020 (Fig. 2I–J, 3I–J) is moderately thin and lacks its posterolateral portion. Due to the anteroposterior length of this element and the absence of clearly visible sutures, it is not possible to exclude that a portion of the entoplastron is present. The ptychogasterid spike is preserved and distinctly protruding in anterior direction. The anterior edge of the epiplastron is slightly convex in dorsal view. The overlap of the gular and humeral scutes on the dorsal surface of the epiplastron is relatively well developed. The epiplastral dorsal lip is 2.8 times wider than long. In dorsal view, it is very little concave medially and slightly thickened and longer medially to the gulohumeral sulcus. The posterior edge of the lip is concave, being the anteroposterior width decreasing in medial direction. The gular is triangular, slightly longer than wide. Its relationships with the entoplastron are unclear due to the absence of visible sutures.

Ptychogaster (Temnoclemmys) batalleri (Bergounioux, 1931)

(Figs. 4–8)

1926 *Emys egarensis* Bataller: 159 (nomen nudum).

1926 *Testudo* sp.: Bataller: pl. 3 figs. 1–2.

1931 *Clemmys batalleri* Bergounioux: 72, figs. 1–5 (original description).

1937 *Clemmys batalleri* Bergounioux, 1931: Bergounioux: 793.

1938 *Clemmys batalleri* Bergounioux, 1931: Bergounioux: 283.

1956 *Clemmys batallery* [sic] Bergounioux, 1931: Bataller: 21.

1957a *Temnoclemmys batalleri* (Bergounioux, 1931): Bergounioux: 1237 (new combination with invalid genus designation).

1957a *Temnoclemmys vallesensis* Bergounioux: 1237 (original description).

1957a *Temnoclemmys elongata* Bergounioux: 1237 (original description).

1957b *Temnoclemmys batalleri* (Bergounioux, 1931): Bergounioux: 40.

1957b *Temnoclemmys vallesensis* Bergounioux: 40.

1957b *Temnoclemmys elongata* Bergounioux: 40.

1957c *Temnoclemmys batalleri* (Bergounioux, 1931): Bergounioux: 164.

1957c *Temnoclemmys vallesensis* Bergounioux: 164.

1957c *Temnoclemmys elongata* Bergounioux: 164.

1958 *Temnoclemmys batalleri* (Bergounioux, 1931): Bergounioux: 185, figs. 18–19, pls. 35–36 (new combination with valid genus designation as its type species).

1958 *Temnoclemmys vallesensis* Bergounioux: 191, figs. 22–23, pls. 38–39.

1958 *Temnoclemmys elongata* Bergounioux: 194, fig. 24, pl. 40.

1958 *Testudo celonica* Bergounioux: 171, figs. 13–14, pls. 30–31 (original description).

1974 *Testudo (Testudo) celonica* Bergounioux, 1958: Aufenberg: 198.

1976 “*Mauremys*” *batalleri* (Bergounioux, 1958): Jiménez: 123.

1977 *Ptychogaster (Temnoclemmys) batalleri* (Bergounioux, 1931): de Broin: 239, fig. 100, pl. 23 figs. 1–4 (new combination).

1977 *Ptychogaster (Temnoclemmys) cf. batalleri* (Bergounioux, 1931): de Broin: 239, pl. 23 figs. 9–14.

1991 *Ptychogaster (Temnoclemmys) batalleri* (Bergounioux, 1931): Jiménez Fuentes and Martín de Jesús: 100.

1991 *Ptychogaster celonica* (Bergounioux, 1958): Jiménez Fuentes and Martín de Jesús: 102 (new combination).

2000 *Ptychogaster (Temnoclemmys) batalleri* (Bergounioux, 1931): Lapparent de Broin: 243, fig. 9 (emended diagnosis).

Emended diagnosis: A species of *Temnoclemmys* displaying all the features included in the diagnosis of this subgenus above, and further characterized by a trapezoidal, very thick and medially slightly concave dorsal epiplastral lip. It therefore differs from *P. (T.) bardenensis* by the medially less concave and much thicker dorsal epiplastral lip throughout its width, and from *P. (T.) cayluxensis* by the more trapezoidal and non-protruding contour of the anterior plastral lobe (due to the straight instead of convex gular angles), and the shorter dorsal epiplastral lip without a thickened inverse triangle.

Syntypes: Bergounioux (1931) described this species on the basis of two fossil remains that are currently lost (see below): an anterior portion of plastron (entoplastron and both epiplastra; Bataller, 1926: pl. 3 figs. 1–2; Bergounioux, 1931: figs. 1–2; see also our Figs. 4A–B, 5A–B); and a shell fragment including two peripheral plates (left peripherals 7–8; Bergounioux, 1931: figs. 3–4; see also our Figs. 4C–D, 5C–D). It is uncertain whether these two plates belong to a single individual. Given that Bergounioux (1931) did not designate a holotype, these two specimens must be considered syntypes. In order to clarify the taxonomic identity of this taxon, we think it is necessary to designate the most complete specimen (Figs. 4A–B, 5A–B) as the lectotype, so that the fragment with the marginal plates (Figs. 4C–D, 5C–D) must be considered a paralectotype. The lectotype was referred to as MGSM139663 by Jiménez Fuentes and Martín de Jesús (1991), and included in the catalogue of the MGSM published by Calzada and Urquiola (1992: 107). However, as noted by Jiménez Fuentes in Adserà and Calzada (2009: 22), this was a mistake, since Jiménez Fuentes and Martín de Jesús (1991) were referring to a different specimen from Sant

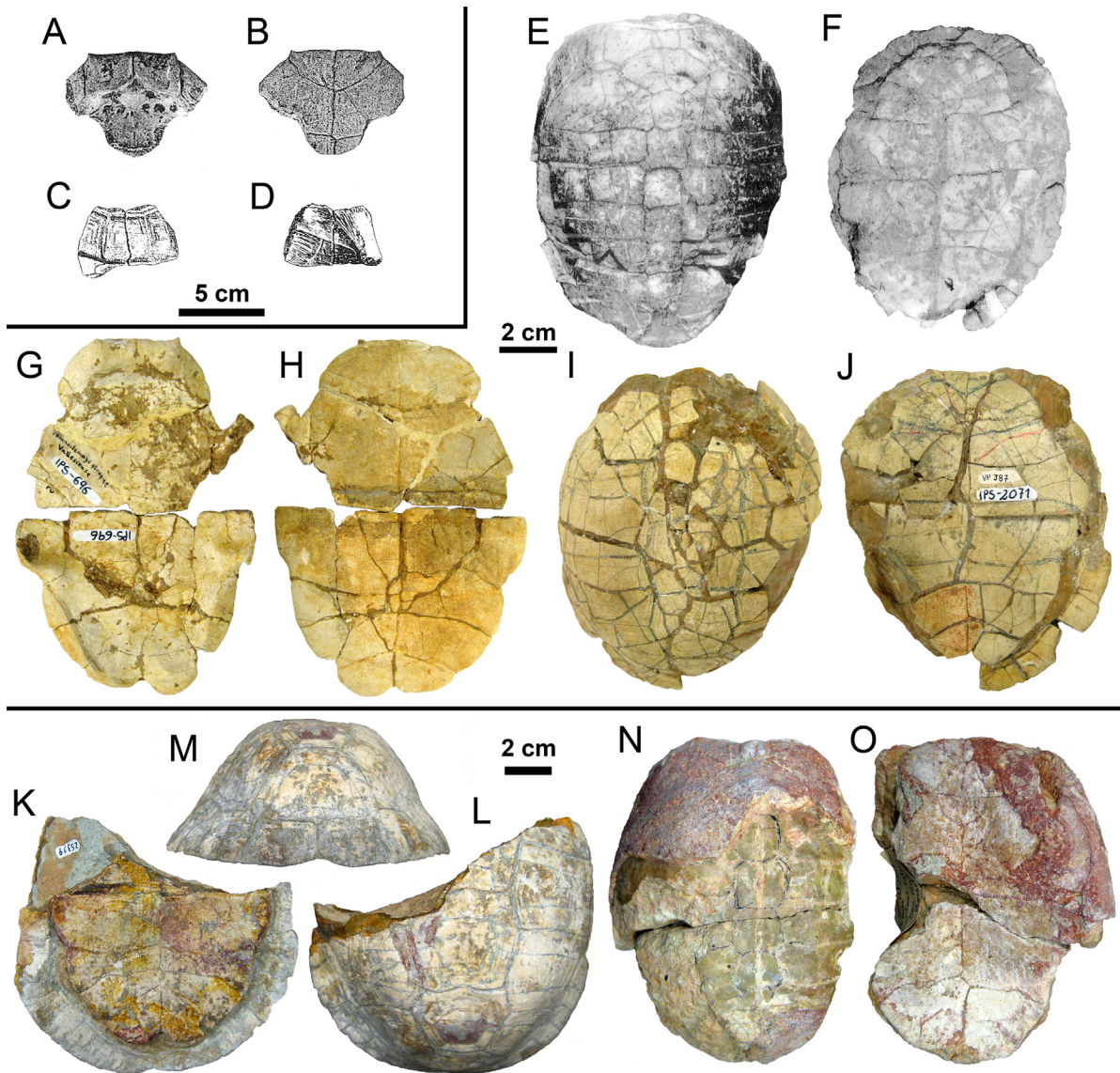


Fig. 4. (Color online). Previously-published shell remains of *Ptychogaster* (*Temnoclemmys*) *batalleri* from the Vallès-Penedès Basin. **A–B**, Lectotype from TS (currently lost; reproduced from [Bataller, 1926](#)), in **A**, dorsal; **B**, ventral views. **C–D**, Paralectotype from TS (currently lost; reproduced from [Bergounioux, 1931](#)), in **C**, external; **D**, internal views. **E**, “Specimen A” from VC (currently lost; reproduced from [Bergounioux, 1958](#): pl. 35), in dorsal view. **F**, “Specimen B” (MGB V32) from VC (reproduced from [Bergounioux, 1958](#): pl. 36), in ventral view. **G–H**, IPS696 from HPS (holotype of *Temnoclemmys elongata* Bergounioux, 1957; see also [Bergounioux, 1958](#): pl. 40), in **G**, dorsal; **H**, ventral views. **I–J**, IPS2071 from VC (holotype of *Temnoclemmys vallesensis* Bergounioux, 1957; see also [Bergounioux, 1958](#): pl. 38–39), in **I**, dorsal; **J**, ventral views. **K–M**, MGS25319A from CR (holotype of *Testudo celonica* Bergounioux, 1958; see also [Bergounioux, 1958](#): pl. 30–31), in **K**, ventral; **L**, dorsal; **M**, posterior views. **N–O**, MGS25319B (paratype of *Testudo celonica* Bergounioux, 1958), in **N**, dorsal; **O**, ventral views.

Fig. 4. (Couleur en ligne). Restes de carapace déjà publiés de *Ptychogaster* (*Temnoclemmys*) *batalleri* du bassin de Vallès-Penedès. **A–B**, Lectotype de TS (actuellement perdu, reproduit à partir de [Bataller, 1926](#)), en vues **A**, dorsale ; **B**, ventrale. **C–D**, Paralectotype de TS (actuellement perdu, reproduit à partir de [Bergounioux, 1931](#)), en vues **C**, externe ; **D**, interne. **E**, « Specimen A » de VC (actuellement perdu, reproduit à partir de [Bergounioux, 1958](#), pl. 35), en vue dorsale. **F**, « Specimen B » (MGB V32) de VC (reproduit à partir de [Bergounioux, 1958](#), pl. 36), en vue ventrale. **G–H**, IPS696 de HPS (holotype de *Temnoclemmys elongata* Bergounioux, 1957; voir aussi [Bergounioux, 1958](#), pl. 40), en vues **G**, dorsale ; **H**, ventrale. **I–J**, IPS2071 de VC (holotype de *Temnoclemmys vallesensis* Bergounioux, 1957; voir aussi [Bergounioux, 1958](#), pl. 38–39), en vues **I**, dorsale ; **J**, ventrale. **K–M**, MGS25319A de CR (holotype de *Testudo celonica* Bergounioux, 1958; voir aussi [Bergounioux, 1958](#), pl. 30–31), en vues **K**, ventrale ; **L**, dorsale ; **M**, postérieure. **N–O**, MGS25319B (paratype de *Testudo celonica* Bergounioux, 1958), en vues **N**, dorsale ; **O**, ventrale.

Quirze, whose correct catalogue number is MGSB31663 (B-27). According to [Bergounioux \(1931\)](#), the syntypes were housed at the Institut Catholique de Toulouse. In 1985, the curators of the MSGB were informed by Drs. Bilotte

and Cugny from the Institut catholique de Toulouse that this material was lost ([Adserà and Calzada, 2009](#)). However, given that there is no evidence that the lectotype has been destroyed, and that it was adequately described and

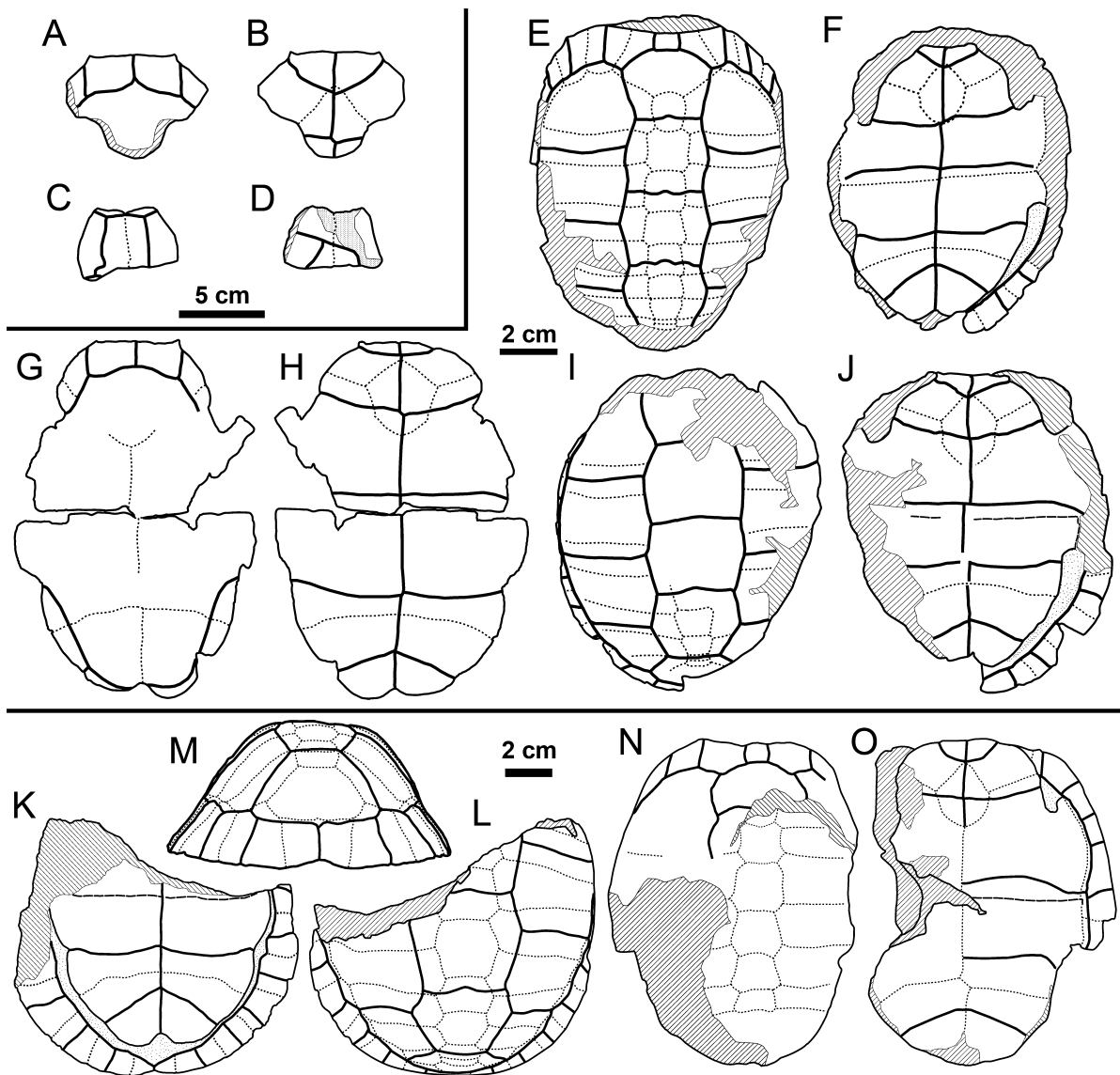


Fig. 5. Schematic drawings corresponding to the fossil remains depicted in Fig. 4. Thick lines correspond to scute sulci, dotted lines denote plate sutures, dashed lines denote completely ligamentous kinesis between hypoplastra and peripherals as well as the hinge between hypoplastron and hypoplastron, dotted areas indicate ligamentous joints, and oblique lines denote missing portions or sediment.

Fig. 5. Dessins schématiques correspondant à des restes fossiles illustrés sur la Fig. 4. Les lignes épaisses correspondent aux sillons des écailles, les lignes pointillées indiquent les sutures de plaques, les lignes pointillées longues indiquent une *kinesis* complètement ligamentaire entre les hypoplastra et les périphériques et aussi la charnière entre l'hypoplastron et l'hypoplastron, les zones en pointillés indiquent des articulations ligamentaires, et les lignes obliques indiquent les portions manquantes ou du sédiment.

figured in the original description of the species, we refrain from designating a neotype.

Type locality: Terrassa (MN10, Late Miocene).

Previously-described material: Partial shell ("specimen A" of Bergounioux, 1958: fig. 18, pl. 35; see also our Figs. 4E, 5E) from VC, which is currently lost; partial shell ("specimen B" of Bergounioux, 1958: fig. 19, pl. 36; see also our Figs. 4F, 5F) from VC, which is currently housed at the MGB (MGB V32); IPS696, partial shell from HPS (Bergounioux, 1958: fig. 24, pl. 40; see also our Figs. 4G–H, 5G–H), which is the holotype of *Temnoclemmys elongata*; IPS2071 (field number VP387), partial

shell from VC (Bergounioux, 1958: figs. 22–23, pls. 38–39; see also our Figs. 4I–J, 5I–J), which is the holotype of *Temnoclemmys vallesensis*; MGSB25319A, partial posterior shell from CR (Bergounioux, 1958: fig. 13–14, pl. 30–31; see also our Figs. 4K–M, 5K–M), which is the holotype of *Testudo celonica*; MGSB25319B, partial shell from CR (Figs. 4N–O, 5N–O; previously not figured by Bergounioux, 1958), which is a paratype of *T. celonica*.

New material: IPS766a–h (Figs. 6A–L, 7A–L), partial shell from EDAR24; IPS64024 (Figs. 6X–Y, 7X–Y), right partial anterior plastral lobe from HP; IPS35267 (Figs. 6V–W, 7V–W), partial anterior plastral lobe

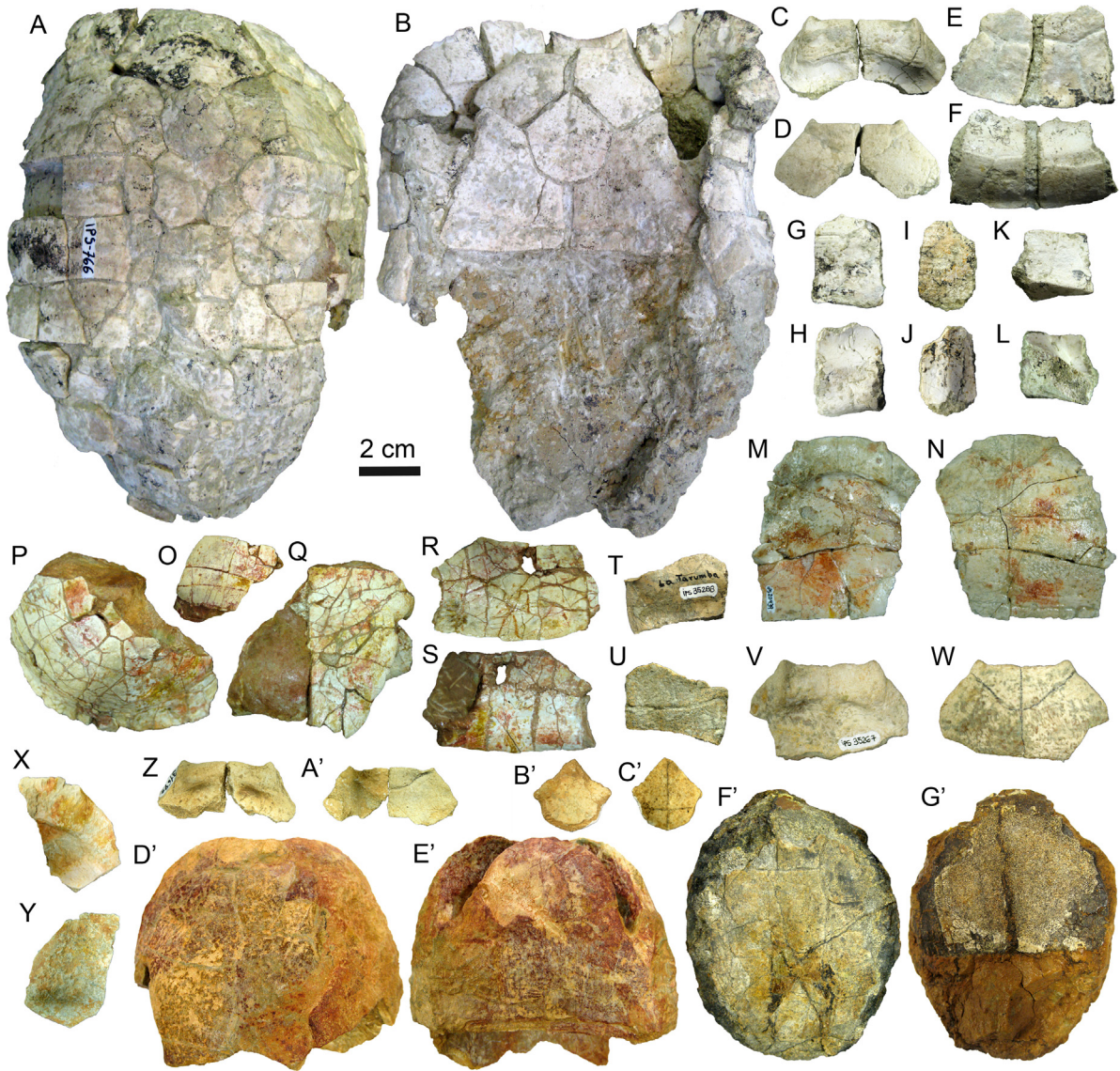


Fig. 6. (Color online.) New shell remains of *Ptychogaster* (*Temnoclemmys*) *batalleri* from various localities of the Vallès-Penedès Basin. **A–L**, IPS766 from EDAR 24; **A–B**, partial shell IPS766a, in **A**, dorsal; **B**, ventral views; **C–D**, Epi IPS766b–c, in **C**, dorsal; **D**, ventral views; **E–F**, left P9–10 IPS766d–e, in **E**, dorsal; **F**, internal views; **G–H**, right P11 IPS766f, in **G**, dorsal; **H**, internal views; **I–J**, right partial P13 IPS766g, in **I**, dorsal; **J**, internal views; **K–L**, left partial P7 IPS766h, in **K**, dorsal; **L**, internal views. **M–N**, anterior plastral lobe IPS20439 from ACM/BDA, in **M**, dorsal; **N**, ventral views; **O–S**, IPS36059 from VC; **O**, partial right P15–6 IPS36059b, in dorsal view; **P–Q**, posterior partial shell IPS36059a,d, in **P**, dorsal; **Q**, ventral view; **R–S**, right peripherals 7–9 and distal portion of pleurals 4–7 IPS36059c, in **R**, dorsal; **S**, internal views. **T–U**, partial left hypoplastron IPS35288 from LT, in **T**, dorsal; **U**, ventral views. **V–W**, partial anterior plastral lobe IPS35267 from VC, in **V**, dorsal; **W**, ventral views. **X–Y**, Partial anterior plastral lobe IPS64024 from HP, in **X**, dorsal; **Y**, ventral views. **Z–A'**, epiplastra MGSB31699 from CM, in **Z**, dorsal; **A'**, ventral views. **B'–C'**, Ento IPS31692 from SMT, in **B'**, ventral; **C'**, dorsal views. **D'–E'**, Partial shell (anterior portion) MGS31662A from CR, in **D'**, dorsal; **E'**, ventral views. **F'–G'**, Partial carapace MGS31662B from CR, in **F'**, dorsal; **G'**, ventral views.

Fig. 6. Restes nouveaux de carapace de *Ptychogaster* (*Temnoclemmys*) *batalleri* de diverses localités du bassin de Vallès-Penedès. **A–L**, IPS766 de EDAR 24; **A–B**, carapace partielle IPS766a, en vues **A**, dorsale; **B**, ventrale; **C–D**, Epi IPS766b–c en vues **C**, dorsale; **D**, ventrale; **E–F**, P9–10 gauches IPS766d–e, en vues **E**, dorsale; **F**, interne; **G–H**, P11 droite IPS766f, en vues **G**, dorsale; **H**, interne; **I–J**, P13 droite partielle IPS766g en vues **I**, dorsale; **J**, interne; **K–L**, P7 partielle gauche IPS766h en vues **K**, dorsale; **L**, interne. **M–N**, lobe plastral antérieur IPS20439 d'ACM/BDA en vues **M**, dorsale; **N**, ventrale; **O–S**, IPS36059 de VC; **O**, P15–6 partielles droites IPS36059b, en vue dorsale; **P–Q**, carapace partielle postérieure IPS36059a,d, en vues **P**, dorsale; **Q**, ventrale; **R–S**, P7–9 et la partie distale des P14–7 droites IPS36059c, en vues **R**, dorsale; **S**, interne. **T–U**, hypoplastron gauche partiel IPS35288 de LT, en vues **T**, dorsale; **U**, ventrale. **V–W**, lobe plastral antérieur partiel IPS35267 de VC, en vues **V**, dorsale; **W**, ventrale. **X–Y**, lobe plastral antérieur partiel IPS64024 de HP, en vues **X**, dorsale; **Y**, ventrale. **Z–A'**, epiplastra MGSB31699 de CM, en vues **Z**, dorsale; **A'**, ventrale. **B'–C'**, entoplastron IPS31692 de SMT, en vues **B'**, ventrale; **C'**, dorsale. **D'–E'**, carapace partielle (portion antérieure) MGS31662A de CR, en vues **D'**, dorsale; **E'**, ventrale. **F'–G'**, carapace dorsale partielle MGS31662B de CR, en vues **F'**, dorsale; **G'**, ventrale.

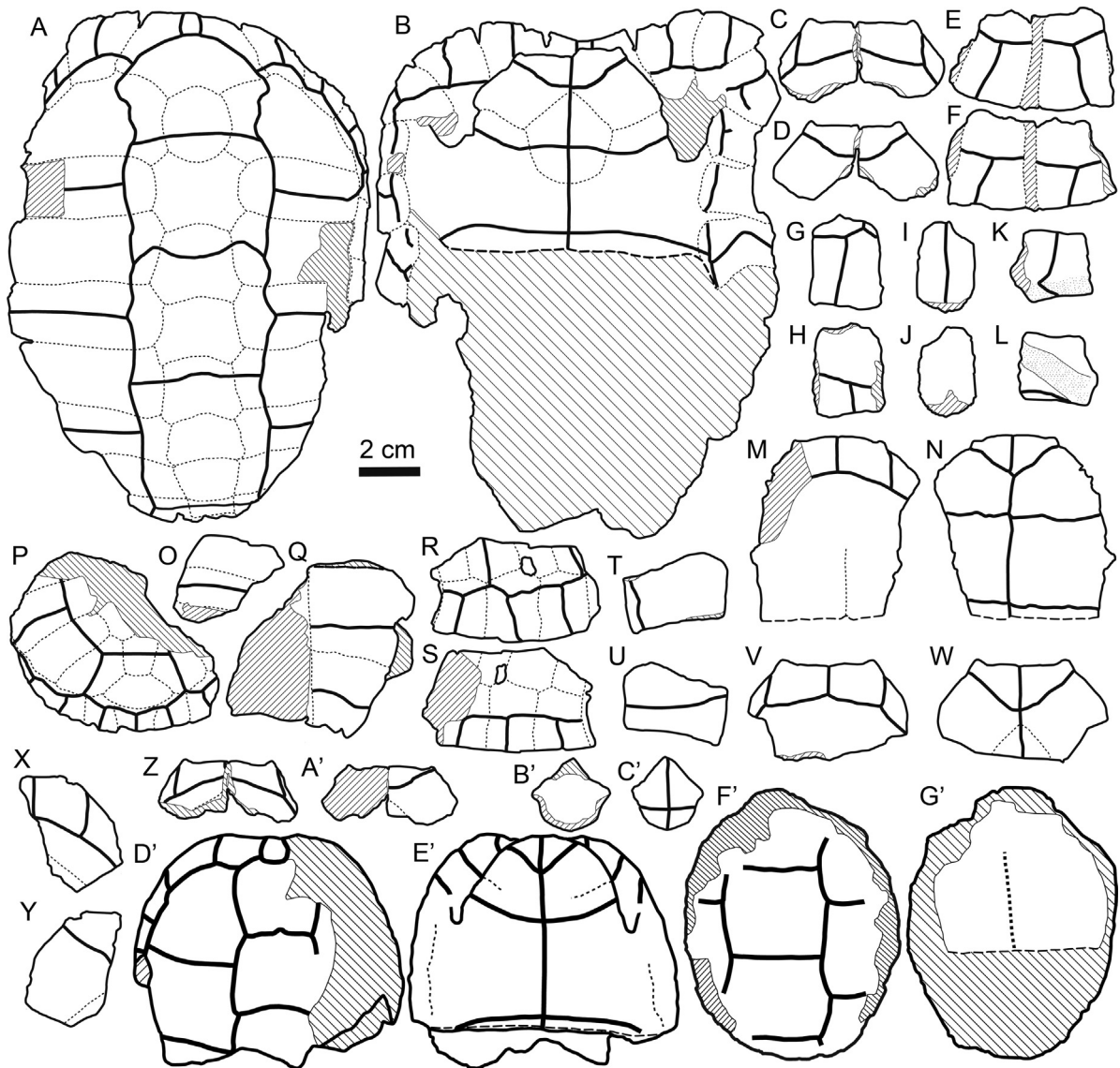


Fig. 7. Schematic drawings corresponding to the fossil remains depicted in Fig. 6. Thick lines correspond to scute sulci, dotted lines denote plate sutures, long dashed lines denote completely ligamentous kinesis between hypoplastra and peripherals as well as the hinge between hypoplastron and hypoplastron, dotted areas indicate ligamentous joints, and oblique lines denote missing portions or sediment.

Fig. 7. Dessins schématiques correspondant à des restes fossiles illustrés sur la Fig. 6. Les lignes épaisses correspondent aux sillons des écailles, les lignes pointillées indiquent les sutures de plaques, les lignes pointillées longues indiquent une *kinesis* complètement ligamentaire entre les hypoplastra et les périphériques, et aussi la charnière entre l'hypoplastron et l'hypoplastron; les zones en pointillés indiquent des articulations ligamentaires, et les lignes obliques indiquent les portions manquantes ou du sédiment.

from VC; IPS20439 (Fig. 6M–N), anterior plastral lobe from ACM/BDA; IPS35288 (Figs. 6T–U, 7T–U), partial left hypoplastron from LT; MGSB31699 (Figs. 6Z–A', 7Z–A'), epiplastron from CM; MGSB31692 (Figs. 6B'–C', 7B'–C'), entoplastron from SMT; IPS36059 (Figs. 6O–S, 7O–S), posterior partial shell from VC; MGSB31662A (Figs. 6D'–E', 7D'–E'), partial anterior shell from CR; MGSB31662B (Figs. 6F'–G', 7F'–G'), partial carapace from CR. The most complete new material corresponds to the three partial shells IPS766, IPS36059 and MGSB31662A.

Stratigraphic range in the Vallès-Penedès Basin: early MN7 + 8 (Middle Miocene) to MN10 (Late Miocene).

Description of the new material from EDAR24: IPS766a (Figs. 6A–B, 7A–B) preserves most of the anterior half of the plastron and most of the carapace, but the posterior area of the latter is in poor condition and not complete; the right xiphiplastron is misplaced and preserved within the matrix filling the carapace, so that only its posterior tip is visible among the right pleural fragments. The two epiplastra IPS766b–c (Figs. 6C–D, 7C–D), left peripherals 9–10 IPS766d–e (Figs. 6E–F, 7E–F), right

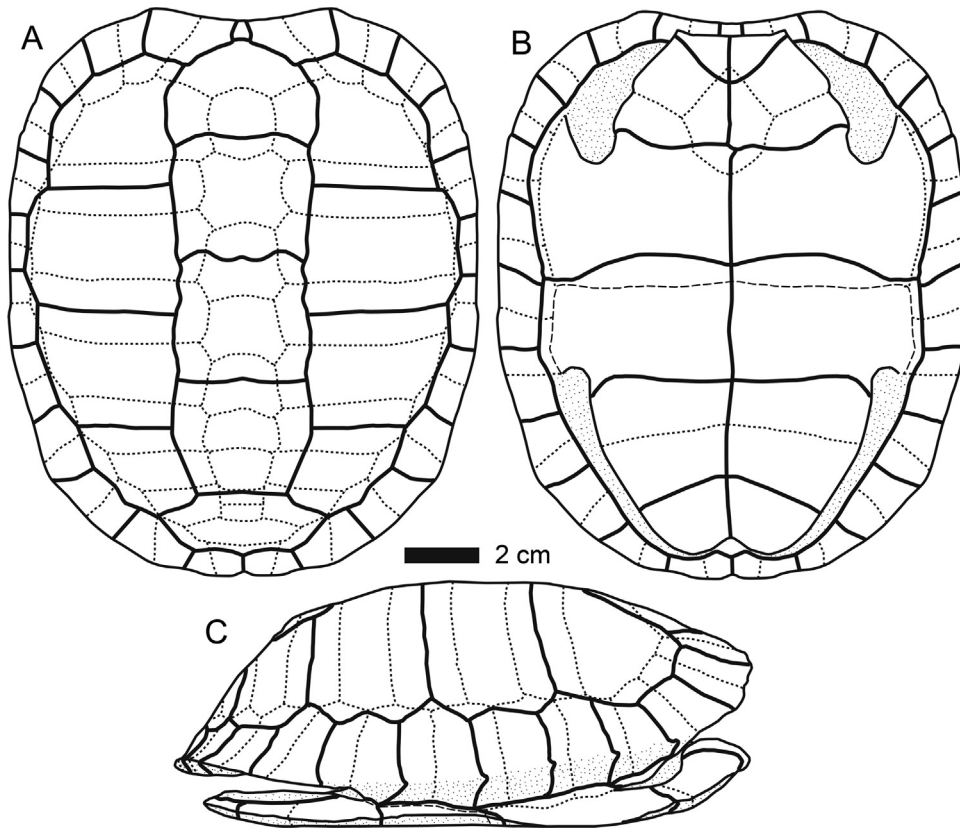


Fig. 8. *Ptychogaster (Temnoclemmys) batalleri* from Vallès-Penedès Basin. Reconstruction of the shell in: **A**, dorsal; **B**, ventral; **C**, right lateral views. Thick lines correspond to scute sulci, dotted lines denote plate sutures, and dashed lines denote completely ligamentous kinesis between hypoplastra and peripherals as well as the hinge between hypoplastron and hypoplastron.

Fig. 8. *Ptychogaster (Temnoclemmys) batalleri* du bassin de Vallès-Penedès. Reconstruction de la carapace en vues : **A**, dorsale ; **B**, ventrale ; **C**, latérale droite. Les lignes épaisses correspondent aux sillons des écailles, les lignes pointillées indiquent les sutures de plaques, et les lignes pointillées longues indiquent une kinesis complètement ligamentaire entre les hypoplastra et les périphériques, ainsi que la charnière entre l'hypoplastron et l'hypoplastron.

peripheral 11 IPS766f (Figs. 6G–H, 7G–H), right distal pleural 3 IPS766g (Figs. 6I–J, 7I–J) and left peripheral 7 IPS766h (Figs. 6K–L, 7K–L) were found associated to IPS766a and belong to the same individual.

The shell is relatively small, low and elongated in lateral view. The decoration of the carapace and plastron surfaces is smooth. The carapace is oval and quite slender, approximately 16 cm long and 13.5 cm wide once reconstructed. IPS766 probably represents a male individual due to the concavity of the hypoplastron and entoplastron. All the scute sulci are visible and the sutures are not obliterated. The carapace does not have evident carinae. As shown by the entoplastron and the hypoplastron, the anterior lobe of the plastron is distinctly bent in dorsal direction.

The nuchal is hexagonal, wider than long and not much concave ventrally. This plate is slightly elongated (ca. 21% of shell length), with the anterior part significantly widened and little emarginated. On the internal surface, there is a transversal moderately developed thickening in correspondence of the edge of the marginal overlap. In lateral view, the dorsal profile of the nuchal is straight, and the anterior edge is slightly arched in anterior view. The neural series is irregular: neural 1 quadrangular, neural 2 octagonal, neurals 3–6 hexagonal with short sides behind, neural

7 is hexagonal, with short sides in front, and neural 8 hexagonal with short sides in front. The pleurals are rectangular, with the length of the lateral edge being equal to that of the medial edge. There is no coincidence (alignment) between pleurals and peripherals in the posterior part of the shell. The peripherals 1–2 are longer than wide, slightly trapezoidal, but without clear strong anterior expansions. Peripherals 3–7 are involved in the bridge and develop a lateral ridge. Peripheral 7 is rectangular, and in internal view it displays the rough, elongated area for the cartilaginous union with the inguinal process. Peripheral 11 is rectangular with an oblique and slightly concave anteromedial border (this is reflected in the shape of the suprapygal 2; see below). The anterior and posterior peripherals are fairly equal in size.

The cervical is relatively small (covering 27% to 30% of the nuchal length), trapezoidal in shape, longer than wide, with the posterior border convex, and with straight lateral edges. The overlap of the cervical on the ventral surface of the nuchal is well developed but relatively short anteroposteriorly; the ventral surface of the cervical is wider than the dorsal one. The vertebral series is present, quadrangular, and slightly narrower than the costal series. Vertebral 1 is lyre-shaped, not covering the lateral corners

of the nuchal and slightly narrower (at its widest point) than the nuchal. Vertebrae 2–4 are quite square, although slightly wider anteriorly than posteriorly. Vertebral 5 is fairly wider posteriorly than anteriorly. The costal series are rectangular, wider than long. The margino-costal sulcus is regularly situated on the peripheral, distal to the pleuro-peripheral suture, except at the level of the bridge (marginals 5, 7 and 9), where the sulcus contacts and in some cases crosses the pleuro-peripheral suture. Marginal 1 is dorsally wider than long; its length exceeds more than half of the anterolateral side of the nuchal. Marginals 2–4 are shorter than marginal 1 and rather square; marginal 4, in particular, has a costo-marginal sulcus situated rather close to the costo-peripheral suture. The ventral overlap of the marginals is well developed.

The anterior plastral lobe is relatively widened, slightly rounded and not completely filling the anterior opening of the shells. The anterior edge is truncated, straight and narrowed if compared to the width of the anterior lobe. The dorsal overlap of the humeral scutes is significant.

The epiplastron is vaguely pentagonal and approximately as wide as long. In dorsal view, the anterior edge of the anterior lobe is approximately rectilinear and laterally bordered by projections anteriorly directed, the ptychogasterid spikes, which are located within the gular shield and triangular, well-developed and distinctly protruding from the epiplastral outline. In anterior view, the edge is located close to the ventral border of the element and it is slightly convex medially. The lateral border of the epiplastron is overall straight but slightly curved close to the epi-hyoplastral suture. In dorsal view, the epiplastral dorsal pad is approximately rectangular (with a concave posterior edge), thrice wider than long; it is characterized by being longitudinally thickened in correspondence of the spike (therefore slightly medial to the gulohumeral sulcus) and moderately concave medially where the thickness of the pad equals that of the plate. However, a depression is developed on the dorsal surface of each epiplastron posteromedially to the gular pad, but laterally to the medial symphysis. In dorsal view, the posterior border of the pad is slightly concave medially (the maximum anteroposterior length corresponds to the longitudinal thickening of the spike), but it is, however, far from the anterior edge of the epiplastron. In lateral view, the epiplastral pad distinctly slopes in anteroventral direction. The area of the ventral surface covered by the gular is distinctly depressed compared to the humeral area.

The entoplastron is only partly developed in the anterior lobe. It is roughly pyriform in shape: the epi-entoplastron sutures are straight and form an angle of about 90°. The entoplastron has a roundish posterolateral edge. The humeropectoral sulcus crosses slightly below mid-height the ventral surface.

The hyoplastra are slightly wider than longer. They contact posteriorly the hypoplastron through a hinge and laterally with peripherals 3–6. The epi-hyoplastral suture is oblique and its lateral end is located rather close to humeropectoral sulcus. The hyo-hyoplastral hinge is straight and approximately transversal; it is located approximately at the mid of peripheral 6.

The gulars are approximately triangular-shaped, fairly short medially and narrow, so that they do not overlap the entoplastron.

The humerals are vaguely pentagonal, slightly longer than wide. The medial length of the humeral is much higher than the medial length of the gular. The humeropectoral sulcus is fairly straight medially but laterally concave anteriorly.

The pectorals are approximately rectangular and wider than long. They contact laterally with peripherals 3–6. The pectoro-abdominal sulcus is medially straight but laterally a little concave in posterior direction. It is located close (from 5 to 7 mm far) to the hyo-hyoplastral hinge but does not contact it. The anterior portion of the abdominal is therefore preserved on the hyoplastron.

Description of the new material from the area of Viladecavalls: IPS35267 (Figs. 6V–W, 7V–W) from VC preserves the epiplastron and part of the entoplastron (possibly also a little portion of the left hyoplastron). The sutures are not visible. Taking into consideration the difference in size, the general morphology of this specimen is congruent with the corresponding region of IPS766b and IPS766c, with the exception of the gulars, which are proportionally wider, more developed in posterior direction and with straighter lateral edges. In anterior view, the ventral edge of the epiplastron is approximately straight and not slightly convex medially as in IPS766. The area of the ventral surface covered by the gular is not depressed if compared to that covered by humeral.

IPS36059a–d (Figs. 6O–S, 7O–S) from VC is a partial posterior shell preserving part of the posterior half of the carapace and the left half of the posterior lobe of the plastron (which is fragmented and partially disarticulated). Both the sutures and the scutes sulci are visible. The specimen is highly fractured, but, thanks to the matrix filling of the shell, all the fragments are not significantly displaced. It includes: IPS36059a, left peripherals 8–11, pygal, suprapygal 1–2, neurals 7–8, left pleurals 6–8, right peripherals 10–11 and right pleural 8 (Figs. 6P–Q, 7P–Q); IPS36059b, partial right pleurals 5–6 (Figs. 6O, 7O); IPS36059c, right peripherals 7–9 and distal portion of pleurals 4–7 (Figs. 6R–S, 7R–S); and IPS36059d, left hyoplastron and xiphoplastron (Figs. 6P–Q, 7P–Q).

The shell is small, slightly high and domed in lateral view. The decoration of the carapace and plastron surfaces is smooth. In dorsal view, the preserved portion of the carapace seems to indicate that it was probably oval and quite slender; at least in the posterior sector of the carapace there are no evident carinae. The neural series is incomplete and the general morphology of this specimen is congruent with the corresponding region of IPS766a with the exception of neural 7, which is octagonal. The shape of the suprapygal 1 is quadrangular and slightly narrowed posteriorly. Suprapygal 2 is triangular, wider than long with rounded latero-posterior edges. The pygal is rectangular, slightly wider than long. In IPS36059a the costo-marginal sulcus shortly intersects the pleural-peripheral suture at the level of the marginals 9 and 11. Vertebral 5 is trapezoid, markedly wider posteriorly than anteriorly (only partially preserved in IPS766a) and partially covers the pygal posteriorly. The sulcus between vertebrae 4–5 laterally does

not cross the suture between pleurals 7–8. Costal 4 is trapezoidal, slightly wider distally. The left portion of the posterior lobe of the plastron (IPS36059d) is narrowed with gently rounded borders. The posterior tip of the xiphiplastron is only partially preserved, but the anal notch should have been reduced (less than 15% of xiphiplastron length), and possibly as wide as long. The dorsal overlap of the plastral scutes is moderately developed, mainly in the area of the femoral scute. The inguinal buttresses are partially preserved and were probably reduced because of the presence of the hinge. The left hypoplastron is rectangular, slightly wider than long. It contacts laterally with peripherals 6–7 through a completely ligamentous union in the inguinal process. The left hypoplastron-xiphiplastron suture is medially straight and laterally slightly curved in posterior direction. The left xiphiplastron is trapezoidal, slightly longer than wide.

The portion of the left abdominal developed on the hypoplastron is entirely preserved and rectangular. The abdominofemoral sulcus is straight (IPS36059d) and antero-laterally does not reach the inguinal process, being located slightly below it. The left femoral is rectangular, wider than long, with the dorsal overlap well developed. The femoroanal sulcus is oblique and faintly sinuous and laterally displays a wide notch. The left anal is triangular, fairly wider than long, and with rounded lateral borders.

IPS35288 (Figs. 6T–U, 7T–U) from La Tarumba only preserves a left posterior partial fragment of hypoplastron that is basically congruent with IPS36059d, from which it differs because the abdominofemoral sulcus is weakly concave anteriorly. Given the scarce morphological details preserved, only a tentative taxonomic attribution is possible for this specimen.

MGSB31692 (Figs. 6B'–C', 7B'–C') from San Miquel de Taudell is a complete entoplastron much smaller than IPS766a but morphologically congruent with it. However, the humeropectoral sulcus is placed more posteriorly in the former than in the latter; the ventral surface is only very slightly curved and therefore the anterior lobe of the plastron to which it belonged was less inclined in dorsal direction.

Description of the new material from the area of Hostalets: IPS64024 (Figs. 6X–Y, 7X–Y) from HP preserves the right epiplastron (possibly also a little portion of the left epiplastron) and a fragment of the right hypoplastron. The epi-hyoplastral suture is not visible and the ptychogasterid spike is not preserved. The general morphology of this specimen is congruent with the corresponding region of IPS766c. However, IPS64024 is slightly smaller and less thick than IPS766c; the dorsal projection of the gular pad is less thick; the gulars are a little longer, with straight lateral edges. The preserved portion of the anterior lobe indicates that this was distinctly bent in dorsal direction.

The anterior plastral lobe IPS20439 (Figs. 6M–N, 7M–N) from ACM/BDA preserves the epiplastron, entoplastron and left and partial right hypoplastron. The sutures are not visible because the skeletal elements are heavily fused together. Taking into consideration the difference in size, the general morphology of this specimen is congruent with the corresponding region of IPS766a with some exception: the gulars are proportionally wider and more developed

in posterior direction and with straighter lateral edges; in dorsal view, the anterior edge of the epiplastron is slightly rounded and not straight as in IPS766a; the hyo-hyoplastral hinge is slightly thinner than IPS766 and oblique (not completely straight as in the latter); the humeropectoral sulcus is slightly sinuous and less curved laterally in anterior direction than IPS766a; the pectoro-abdominal sulcus is slightly oblique and sinuous instead of being completely straight as in IPS766a; and finally, IPS20439 shows the anterior lobe distinctly bent in dorsal direction.

MGSB31699 (Figs. 6Z–A', 7Z–A') preserves both epiplastron and a little portion of the left entoplastron of the same specimen. Even if the general morphology of this specimen is similar to the corresponding region of the much larger IPS766b–c, the following features can be outlined: the gulars are proportionally narrower and slightly less developed in posterior direction and with sinuous lateral edges; in dorsal view, the anterior edge of the epiplastron is slightly rounded and not straight as in IPS766b–c; in ventral view, the ventral edge of the epiplastral pad has a slightly convex profile.

Description of the new material from Sant Celoni: MGSB31662A (Figs. 6D'–E', 7D'–E') from CR preserves the anterior half of the shell and most of the posterior lobe of the plastron, which is housed mostly inside the shell and poorly preserved (not visible in the figure). The two hypoplastra are misplaced and preserved within the matrix filling the carapace, and therefore only their posterior tip is visible in posterior view. The right portion of the dorsal shell is partly covered by a hard concretion. All the scute sulci are visible whereas the sutures are obliterated. Except for its different size and the shell shape, which is relatively high and slightly domed, the general morphology of MGSB31662A is congruent with that of IPS766. The shape of the carapace is less oval and slender than in IPS766, being approximately 10 cm wide and approximately 12 cm long once reconstructed. MGSB31662A probably also corresponds to a male individual, given the concavity of the entoplastron and the hypoplastron. The anterior lobe of the plastron is more distinctly bent in dorsal direction than in IPS766. The nuchal is significantly widened in anterior view, more emarginated and much concave ventrally than in IPS766. In lateral view, the dorsal profile of the nuchal is less straight, much arched at the end of the cervical. The sutures and sulcus of the neural and peripheral series are not visible, and therefore differences in the neural pattern cannot be determined. Peripherals 1–2 are less prominent in anterior direction than in IPS766, but morphologically congruent with it. The cervical is relatively smaller than in IPS766 and has a narrower anterior edge narrower; the overlap of the cervical on the ventral surface of the nuchal is significantly longer anteroposteriorly. The vertebral series are somewhat narrower and vertebral 1 is less lyre-shaped. Marginal 1 is square-shaped and rather rectangular as in IPS766. The anterior plastral lobe of MGSB31662A is slightly narrower than in IPS766, somewhat rounded and not completely filling the anterior opening of the shell. In anterior view, the anterior edge of the anterior plastral lobe is located close to the dorsal border of this element and it is medially quite convex. In dorsal

view, the anterior edge of the anterior lobe is slightly round and laterally bordered by ptychogasterid spikes, which are poorly developed and not protruding from the epiplastral outline. The gulars are triangular-shaped, proportionally longer in posterior direction and with straight lateral edges. The area of the ventral surface covered by the gulars is not depressed if compared to IPS766. In dorsal view, the epiplastral dorsal pad is vaguely trapezoidal, slightly longer in posterior direction than in IPS766. In lateral view, the epiplastral pad distinctly slopes anteroventrally, forming an angle slightly over 45°. The pectoro-abdominal sulcus is medially straight and close to, but not overlapping, the hyo-hypoplastral hinge; laterally it is located close to the hyo-hypoplastral hinge, contacting it at least on the left side.

MGSB31662B (Figs. 6F'–G', 7F'–G') only preserves the central part of the carapace and the anterior part of the plastron, which is completely eroded. In the dorsal region, it preserves completely the vertebrae 2–3 and partially the posterior part of the vertebral 1 and the anterior part of vertebral 4. Vertebral series is rectangular, wider than long and not quadrangular as in IPS766. Furthermore, vertebrae 2–4 are less wide anteriorly. On the basis of the small preserved portion of the C1–C3 area, these elements seem rectangular.

5. Discussion

5.1. Taxonomy and nomenclature of subgenus *Temnoclemmys*

Ptychogaster (*Temnoclemmys*) *batalleri*—the type species of subgenus *Temnoclemmys*—has a complex nomenclatural history. The first name applied to this taxon was *Emys egarensis*, erected by *Bataller* (1926) on the basis of material from TS (see above). The author, however, failed to describe the material, so subsequently *Bergounioux* (1931) considered it to be a nomen nudum. Such a contention is further strengthened by the fact that, although *Bataller* (1926) figured the holotype, he did not refer to it within the text, and in the plate he incorrectly labeled it as *Testudo* sp. *Bergounioux* (1931) therefore described a new species, *Clemmys batalleri*, based on the same specimen. This was accepted by *Bataller* (1956), who nevertheless misspelled the species nomen as “*batallery*” and further incorrectly attributed the authorship to *Bergounioux* (1938) instead of *Bergounioux* (1931).

Later on, *Bergounioux* (1957a) erected the genus *Temnoclemmys* to reallocate *Clemmys batalleri* and three newly-described species of the genus: *Temnoclemmys cordiformis* and *Temnoclemmys vallesensis* from Viladecavalls (MN10), and *Temnoclemmys elongata* from Hostalets de Pierola Superior (MN9). *Bergounioux* (1957a, published in February) described the new taxa without figuring the material, designating a holotype, or indicating which of the species must be considered the type species of the new genus. These results were summarized a few months later by *Bergounioux* (1957b, published in August), who cited the three new species as “sp. nov.” (when in fact they had been already described by himself) and moreover reported (presumably incorrectly) the occurrence of *T. elongata* from both HP and VC. A third paper, published by the same

author in the same year (*Bergounioux*, 1957c), is merely a translation into Spanish of his former paper in French (*Bergounioux*, 1957a).

According to the Code (ICZN, 1999, Art. 13.1) the descriptions provided by *Bergounioux* (1957a) suffice the requirements for these species nomina to be valid. In contrast, this publication does not fulfill the requirements of Art. 68 regarding the fixation of a type species, so that the genus-group name *Temnoclemmys* *Bergounioux*, 1957 is not nomenclaturally valid (Art. 13.3). *Bergounioux* (1958) described again (and in greater detail) the genus *Temnoclemmys* as “nov. gen.”, together with the four species that he distinguished among this genus: *T. batalleri* from TS and VC; *T. cordiformis* and *T. vallesensis* from VC; and *T. elongata*, only from HPS. *Bergounioux* (1958) explicitly designated *T. batalleri* as the type species (“genotype”) of *Temnoclemmys*, and further described and figured the remaining three species. Accordingly, the authorship of the genus must be attributed to *Bergounioux* (1958), instead of any of his three preceding publications appeared the year before (contra *Lapparent de Broin*, 2000, who attributed the authorship of *Temnoclemmys* to *Bergounioux*, 1957).

Jiménez (1976) considered that both *Temnoclemmys* and the various species of this genus erected by *Bergounioux* (1958) were not taxonomically valid, and referred to them all as “*Mauremys*” *batalleri*. *de Broin* (1977), in contrast, considered *Temnoclemmys* as a valid subgenus within the genus *Ptychogaster* *Pomel*, 1847, and her proposal was subsequently followed by *Jiménez Fuentes and Martín de Jesús* (1991) as well as by *Lapparent de Broin* (2000). In this regard, it should be noted that the material from Venta del Moro attributed to “*Mauremys*” cf. *batalleri* by *Jiménez* (1976) does belong in fact to *Mauremys* sp. (*Lapparent de Broin*, 2000). *Jiménez Fuentes and Martín de Jesús* (1991) explicitly considered that *T. vallesensis* and *T. elongata* are synonyms of *P. (T.) batalleri*, but concluded that *T. cordiformis* must be considered a nomen nudum. In contrast, *Lapparent de Broin* (2000) (see also *de Broin*, 1977) considered that these three nominal taxa would be junior subjective synonyms of *P. (T.) batalleri* (*Bergounioux*, 1931), for which *Lapparent de Broin* (2000) provided an emended diagnosis.

Currently, three different valid species of the subgenus *Temnoclemmys* are recognized (*Lapparent de Broin*, 2000; *Murelaga et al.*, 1999, 2002): *P. (T.) cayluxensis*, from the Oligocene of France; *P. (T.) bardenensis*, from the Early Miocene of Spain; and *P. (T.) batalleri*, from the Middle to the Late Miocene of Spain and France. The scarce and fragmentary material available for *P. bardenensis* (*Murelaga et al.*, 1999, 2002) and *P. cayluxensis* (*Lapparent de Broin*, 2000, p. 244; *Lydekker*, 1889) precludes evaluating some of the features that we consider diagnostic of subgenus *Temnoclemmys*, namely: the length of the peripherals 1–2; the length of the nuchal and the shape of the posterior lobe of the plastron (in the two above-mentioned species); and the length of the cervical (only not preserved in *P. cayluxensis*). However, other features preserved in these taxa—small size, contour of the anterior lobe of the plastron, shape of the epiplastral lip, and in *P. bardenensis* also the length of the cervical—enable an unambiguous attribution of these species to the subgenus *Temnoclemmys* instead of

Ptychogaster s.s. On the other hand, differences compared to *P. (T.) batalleri* (see our emended diagnosis for the latter species above) confirm the distinct species status of both *P. (T.) cayluxensis* and *P. (T.) bardenensis*. In particular, the morphology of the epiplastral lip enables to distinguish the latter two species (both between one another, and also from the type species of *Temnoclemmys*), whereas the morphology of the anterior lobe of the plastron further enables to distinguish *P. cayluxensis* from the remaining two species of this subgenus. Overall, in spite of the scarcity of the available material for *Temnoclemmys* species other than *P. (T.) batalleri*, their preserved morphology enables an attribution to this subgenus and also confirms their distinct species status—in further agreement with their older age.

A fourth nominal taxon, *Ptychogaster francofurtanus* Reinach, 1900 from the Miocene of Germany, might be also attributable to subgenus *Temnoclemmys*. This binomen is nomenclaturally valid, even though (to our knowledge) it has not been employed by subsequent authors after its original description. This species was erected on the basis of several shell remains—peripherals 5–9 (Reinach, 1900: pl. 20 figs. 1–2), a partial nuchal (Reinach, 1900: pl. 20 fig. 3), the anterior portion of the plastron (Reinach, 1900: pl. 20 figs. 4–6)—most likely attributable to a single individual, and recovered from the MN3 locality of Frankfurt-Nordbassin (Reinach, 1900: 56–58). The ligamentous area in peripheral 7 confirms an attribution to *Ptychogaster* s.l., whereas the short cervical further suggests an attribution to *Temnoclemmys*. Among the species of the latter genus, the material described by Reinach (1900) most closely resembles *P. (T.) batalleri* in the morphology of the anterior portion of the plastron, differing from *P. (T.) bardenensis* by the less concave dorsal epiplastral lip that is also thicker throughout all of its width, and from *P. (T.) cayluxensis* by the straighter and non-protruding anterior margin. However, due to incomplete preservation, the tapering of the posterior lobe of the plastron characteristic of *Temnoclemmys* cannot be ascertained in *P. francofurtanus*. We therefore consider that the morphology preserved by the holotype and only known specimen of this taxon is insufficient to conclude that it belongs to the same species than *P. (T.) batalleri*, and that additional remains would be required to confirm its tentative attribution to subgenus *Temnoclemmys*. We consequently conclude that *P. (?Temnoclemmys) francofurtanus* Reinach, 1900 is currently best considered a nomen dubium—i.e., a nomenclaturally valid name of doubtful taxonomic application. If additional material shows that *P. francofurtanus* is a senior subjective synonym of *P. (T.) batalleri*, Reinach's (1900) name would take precedence. This would go against prevailing usage and might cause confusion, but given that the provision of Article 23.9.1.1 of the Code (“the senior synonym. . . has not been used as a valid name after 1899”) cannot be fulfilled, reversal of precedence would not be possible without referring the case to the International Commission on Zoological Nomenclature (ICZN: article 23.9.3).

Two of the three nominal species of *Temnoclemmys* erected by Bergounioux (1957a)—*T. elongata* and *T. vallesensis*—are attributable to subgenus *Temnoclemmys* because they display the diagnostic features of this subgenus (e.g., very thick dorsal epiplastral lip, short cervical,

trapezoid anterior margin of the plastron and tapering posterior margin of the plastron; see diagnosis above for further details). Moreover, the two above-mentioned nominal taxa are considered here junior synonyms of *P. (T.) batalleri*, because they display the same morphology of the dorsal epiplastral lip and of the anterior margin of the plastron—which enable a distinction of this species from both *P. bardenensis* and *P. cayluxensis*. Therefore, the minor differences originally employed by Bergounioux (1957a, 1958) to distinguish these species (based on the shape of the carapace) are not considered diagnostic, being merely attributable to sexual dimorphism or intraspecific variability. In contrast, we conclude that the nominal taxon *T. cordiformis* Bergounioux, 1957a must be considered a nomen vanum, instead of a junior subjective synonym of *P. batalleri* as suggested by Lapparent de Broin, 2000. *Temnoclemmys batalleri* was originally erected by Bergounioux (1957a: 1237; see also Bergounioux, 1957b: 40, 1957c: 164, 1958: 189, figs. 20–21, pl. 37) on the basis of a partial shell without number from VC from the former Villalta's collection—which, according to Jiménez Fuentes and Martín de Jesús (1991), is currently lost. Jiménez Fuentes and Martín de Jesús (1991) concluded that, given the meager description provided by Bergounioux (1958) and the loss of the holotype, *T. cordiformis* should be considered a nomen nudum. In fact, based on the authors' reasoning (according to which the remains used to erect the species cannot even be identified at the family level), *T. cordiformis* should be considered instead a nomen vanum. The holotype of this nominal taxon is poorly preserved and further displays the neural plates displaced to the left side relative to the vertebral scutes. Bergounioux (1958) attributed the displacement to taphonomic distortion, when in fact this more likely reflects some kind of pathology. In any case, based on the description and figures provided by Bergounioux (1958), this specimen cannot correspond to a ptychogasterine—as indicated by the lack of ptychogasterid spikes, the situation of the humeropectoral sulcus below the entoplastron (without any overlap), and the rounded (instead of markedly elongate) shape of the shell (about 10 cm in length and 9 cm in width). Moreover, the possession of a hexagonal (instead of octagonal) neural 2 further conclusively discounts an attribution to the genus *Ptychogaster*. The specimen might belong to a testudinid or to a non-ptychogasterine geoemydid, and even if it was not lost, it is probably too poorly preserved to be able to discern its taxonomic affinities. Therefore, the nominal taxon *T. cordiformis*, although nomenclaturally valid, is here considered a nomen vanum.

5.2. Taxonomic attribution of the described remains

***Ptychogaster (Temnoclemmys) batalleri*:** Most of the new ptychogasterine material from the Vallès-Penedès described here can be ascribed to *P. (T.) batalleri*. This is the case not only for the material coming from the areas of Viladecavalls and els Hostalets, but also from the partial shell from EDAR in the area of Sabadell. The latter shows a short cervical and a slightly elongated nuchal, together with the same general morphology of the dorsal epiplastral lip, that characterize *P. (T.) batalleri*. Regardless

of the difference in size, IPS766 displays a much wider, shorter and less concave shell compared to *Ptychogaster* s.s., being morphologically similar to the classical material of *P. (T.) batalleri*, such as IPS2071, MGSB25319B, MGSB31662B and specimens A and B from VC. The new material from the area of Viladecavalls, in turn, can be attributed to *P. (T.) batalleri* on the basis of the trapezoidal contour of the anterior plastral lobe as well as the morphology of the dorsal epiplastral lip (in the case of IPS35267), and based on the narrowing of the posterior lobe of the plastron (in the case of IPS36059 and IPS35288). The newly reported material from ACM, CM and HP can be similarly ascribed to *P. (T.) batalleri* based mainly on the morphology of the epiplastral dorsal lip, which resembles that of the lectotype as well as of IPS696 from HPS. The new material from the area of Hostaletes (IPS64024, IPS20439 and MGS31699) shows a trapezoidal dorsal epiplastral lip that is thick throughout its width, little concave and medially narrower, which discounts an alternative attribution to *P. (T.) bardenensis* or *P. (T.) caulexensis*. The new material from ACM, in the area of els Hostaletes, further enables to conclusively show that *P. (T.) batalleri* was already present from the early MN7+8 onwards in the Vallès-Penedès Basin, which was not possible to ascertain on the basis of the previously-available material from this area, due to stratigraphic provenance uncertainties. This agrees with the range of *P. (T.) batalleri* in France (Hervet, 2003; Lapparent de Broin, 2000), where it is already recorded in the Middle Miocene localities of Sansan (MN6) and La Grive-Saint-Alban (MN7+8)—further extending into the Turolian, as recorded in the sites of Aubignas I (MN11) and Aubignas II (MN12).

Most significantly, the new material reported here from Can Rabassa helps to solve a long-lasting taxonomic problem regarding another taxon erected by Bergounioux, namely *Testudo celonica* Bergounioux, 1958. This species was described on the basis of Vallesian material from CR in Sant Celoni (holotype MGSB25319A; see Jiménez Fuentes and Martín de Jesús, 1991), which had been first figured (but not described) as a “new turtle” from Sant Celoni by Bataller (1956: pls. 1–4). Auffenberg (1974) considered that this taxon was likely a junior subjective synonym of *Testudo antiqua* Bronn, 1831, but Jiménez Fuentes and Martín de Jesús (1991) reassigned it to the genus *Ptychogaster*. This attribution was later confirmed by Lapparent de Broin (2000), according to whom the holotype of “*Testudo*” *celonica* would belong to *Ptychogaster* s.s. The new material reported here from the type locality, however, leads us to conclude that this taxon must be assigned instead to the subgenus *Temnoclemmys*, and in particular to *P. (T.) batalleri*. Such a contention is supported by the shorter cervical, slightly elongated nuchal, the absence of the well-developed peripherals 1–3, and the hexagonal neural 4, among other features related to the dorsal epiplastral lip. Accordingly, we conclude that *Testudo celonica* is but another junior subjective synonym of *P. (T.) batalleri*.

Ptychogaster (Temnoclemmys) sp.: Among the newly reported material, a few specimens can be attributed to the subgenus *Temnoclemmys* but must be left unassigned at the species level. These remains display the main

autapomorphy of *Temnoclemmys*—trapezoidal and thick dorsal epiplastral lip (Lapparent de Broin, 2000; Murelaga et al., 2002)—as well as other features of this subgenus, such as the lack of well-developed peripherals 1–2 with strong anterior expansions and reduced axillary buttresses (Hervet, 2003, 2006). The Vallès-Penedès specimens are similar to those of *P. (T.) bardenensis* from the slightly older locality of Las Bardenas (MN3) in Spain (Murelaga et al., 1999, 2002), as shown by the slightly narrow, short and trapezoidal dorsal epiplastral lip, as well as the slightly protruding anterior edge of the anterior plastral lobe. However, IPS64020 differs from *P. (T.) bardenensis* by the medially less concave and much thicker dorsal epiplastral lip throughout its width (Murelaga et al., 1999, 2002). This would in principle discount an attribution to this species, although it should be taken into account that such a feature is quite variable in *P. (T.) batalleri* from the Vallès-Penedès Basin (see above). In turn, the fragmentary new remains from CC may be attributable to either *P. (T.) batalleri* or *P. (T.) bardenensis*, because the peripheral series is unknown for the latter species. Therefore, we refrain from providing a specific attribution for these remains, which in any case constitute the oldest record of the subgenus *Temnoclemmys* in the Vallès-Penedès Basin—its first appearance datum in this basin being as old as that of *Ptychogaster* s.s. (see below).

Ptychogaster (Ptychogaster) sp.: Finally, some of the described specimens are attributable to the genus *Ptychogaster*—as indicated among others by the completely ligamentous union between hypoplastron and peripherals and the presence of a hinge between hyoplastron-hypoplastron (Hervet, 2006; Murelaga et al., 2002) in IPS64019—and more specifically to subgenus *Ptychogaster*—based on the presence of elongated nuchals and very narrow and elongated dorsal epiplastral lip, as well as on the lack of the diagnostic features of *Temnoclemmys*. Moreover, the dimensions of the available fragmentary remains suggest a shell size consistent with species of subgenus *Ptychogaster*, but larger than those of *Temnoclemmys*.

The described specimens from the Early Miocene of Can Canals and El Canyet are very similar to those of *P. (P.) ronheimensis* from the MP22 (Early Oligocene) of Germany (Groessens-Van Dyck and Schleich, 1985) and the MN3 (Early Miocene) of Spain (Murelaga et al., 1999). Similarities include the relatively large size and slenderness of the peripheral 7 of IPS64019—much more robust in *P. sansaniensis*; the narrow and not markedly convex contour of the anterior plastral lobe of IPS64018 (wider and more convex in *P. sansaniensis*); and the slightly narrow and relatively short epiplastral lip of IPS64018 (narrower and more elongated in other species of *Ptychogaster* s.s.). In spite of these similarities with *P. (P.) ronheimensis*, the anterior edge of the anterior plastral lobe of IPS64018 is more concave than in the specimens from the type locality (Ronheim), in which it tends to be transversally or medially protruding, thus more closely resembling the Spanish specimens attributed to the same species and also those of *P. (P.) sansaniensis* from France. The lack of preservation of other diagnostic features of *P. (P.) ronheimensis*—the hexagonal neural 4 (instead of octagonal as in *P. griepiacensis*

and *P. emydoides*), the position of the humeropectoral sulcus coinciding with the entoplastron-hyoplastron suture (instead of being situated in the middle of the entoplastron as in *P. sansaniensis*), and the wide and anteriorly little convex plastron (instead of wider and more convex, filling more extensively the openings of the shell, as in other species of *Ptychogaster* s.s.)—hinders an attribution to the species level for the EC and CC material.

The younger material from els Hostalets de Pierola, in turn, can be attributed to *Ptychogaster* s.s. on the basis of the following features (Hervet, 2006): the narrow anterior edge of the anterior plastral lobe as well as elongated epiplastral lip in IPS64022; and the presence of a pair of pronounced thickenings on ventral face of nuchal in IPS64023. Both specimens are very similar to those of *P. (P.) sansaniensis* from MN6 of Sansan (France). Thus, IPS64022 resembles the latter species in the dorsally-elongated (quadrangular) epiplastral lip, but differs from it regarding the length of the gulars—proportionally longer and covering the anterior portion of the entoplastron in IPS64022, whereas in *P. sansaniensis* they are very elongated (at least twice longer than the humeral; Lapparent de Broin, 2000). IPS64023, in turn, resembles *P. sansaniensis* in the large cervical, the well-developed of the internal ventral overlap of cervical, and the anteriorly narrow vertebral 1. The two former features are synapomorphies shared with *P. emydoides* (so they cannot unequivocally confirm an attribution to *P. sansaniensis*), whereas the shape of the vertebral 1 is a highly variable feature, as shown by the specimens from MN2 of Saint-Gerand-le-Puy in France (de Broin, 1977).

Although the available remains of *Ptychogaster* s.s. from the Vallès-Penedès Basin are too scarce to provide a taxonomic assignment at the species level, they enable for the first time the report of this subgenus from this basin. The material from EC and CC, which shows some resemblances to *P. ronheimensis*, indicates that *Ptychogaster* s.s. was already recorded in the Vallès-Penedès by the late Early Miocene. The material from els Hostalets de Pierola, in contrast, shows some more derived features within this subgenus and is thus closer to *P. sansaniensis* and *P. emydoides*. IPS64022 indicates that this subgenus was recorded in the Vallès-Penedès Basin until at least the Late Aragonian (MN7+8), although an Early Vallesian (MN9) age cannot be excluded for IPS64023.

5.3. The distinctiveness of *Temnoclemmys*

Temnoclemmys has been considered a neotenic form compared to other *Ptychogaster* (Lapparent de Broin, 2000; see also Murelaga et al., 2002), in spite of being distinguishable from juveniles of the latter in several features, such as a short cervical in dorsal and internal view, slightly narrowed and short dorsal epiplastral lip, narrower posterior lobe of the plastron, wider nuchal, and lack of well-developed peripherals 1–2 with strong anterior expansions. Hervet (2006) and Murelaga et al. (2002) considered that *Temnoclemmys* would be neotenic (and, hence, a pedomorphic, or juvenilized, form) compared to *Ptychogaster* s.s. merely based on the reduced adult size (small specimens with

well closed, often obliterated sutures), as well as the short anal notch with straight borders, of the former. The size of the anal notch may be variable among individuals and related to sexual dimorphism, regardless of ontogenetic stage, as shown by some extant geoemydids (Pritchard, 2008). Moreover, the new material from EDAR described here indicates that differences in size between the two subgenera are less marked than previously thought. In fact, size in itself is not a valid criterion for inferring the polarity of heterochronic change (Alba, 2002). The latter must be based instead on whether a particular taxon displays a juvenilized (pedomorphic) or overdeveloped (peramorphic) morphology (irrespective of size) compared to its presumed ancestor (Alba, 2002; Alberch et al., 1979; Gould, 1977). Without a sound phylogenetic hypothesis and ontogenetic data for these taxa, it is not even possible to determine the polarity of heterochronic change, so that the neotenic hypothesis for *Temnoclemmys* remains to be tested.

Taxonomically, the subgenera *Ptychogaster* and *Temnoclemmys* can be distinguished based on several features, as shown by the diagnoses provided in this paper. However, their phylogenetic relationships remain uncertain. Hervet (2006) performed a preliminary cladistic analysis of several western European *ptychogasterines*, but explicitly refrained from including *Temnoclemmys* because of its purported pedomorphic status—which, according to this author, would create problems for the definition and polarization of characters. Hervet (2006) did, however, not explain what problems the purported pedomorphosis (i.e., juvenilization) of *Temnoclemmys* imposed on phylogenetic reconstruction. Recently, a preliminary cladistic analysis based on Hervet's (2006) matrix, but further incorporating *P. (T.) batalleri*, supported a sister-taxon status between *Temnoclemmys* and *Ptychogaster* s.s., although the internal phylogeny of the latter subgenus was not fully resolved (Luján et al., 2013b). This is consistent with the results of this paper, which show that *Temnoclemmys* and *Ptychogaster* can be distinguished from one another on the basis of morphologic shell features.

The use of subgenera is not very frequent in testudinoid systematics. This fact raises the issue of whether *Ptychogaster* and *Temnoclemmys* might be better distinguished at the genus instead of subgenus rank. Here, we maintain the distinction between these taxa at the subgeneric level, in agreement with the usage by previous authors (Hervet, 2003; Lapparent de Broin, 2000, 2001; Murelaga et al., 1999, 2002), because the shell characters that distinguish the two taxa are not very numerous. This fact notwithstanding, a more extensive study, further incorporating cranial and non-shell postcranial features (currently unknown for *Temnoclemmys*) might eventually support elevating the latter taxon at the genus rank. In order to do so, a more comprehensive cladistic analysis—incorporating not only more characters but also a wider representation of both extinct and extant geoemydids than in Hervet (2006)—would be required in order to confirm the sister-taxon relationship between *Temnoclemmys* and *Ptychogaster* s.s., as well as to test the purported monophyly of the *Ptychogasterinae* and their phylogenetic position among the *Geoemydidae*.

6. Summary and conclusions

The following *Ptychogasterinae* are recorded in the Vallès-Penedès Basin: *Ptychogaster* (*Ptychogaster*) sp. (MN4, MN7 + 8 and MN9?), representing the first record of subgenus *Ptychogaster* from this basin; *P. (Temnoclemmys)* sp. (MN4), indicating that the first appearance datum of subgenus *Temnoclemmys* is at least as old as that of the nominotypical one; and *P. (T.) batalleri* (MN7 + 8 to MN10), including most of the described material, and unequivocally showing the presence of this taxon also in the late Middle Miocene. Although some of the newly reported remains attain a larger size than previously recorded, the morphology of the studied specimens supports that a single species of *Temnoclemmys* is present in the Vallès-Penedès Basin during the Late Aragonian and Vallesian. Previously-unpublished material further indicates that *Testudo celonica* is another junior synonym of *P. (T.) batalleri*, like the nominal taxa *Temnoclemmys elongata* and *Temnoclemmys vallesensis*. In contrast, *Temnoclemmys cordiformis* is considered a nomen vanum of uncertain taxonomic affinities, whereas *Ptychogaster francofurtanus* is tentatively assigned to subgenus *Temnoclemmys* and provisionally considered a nomen dubium.

Acknowledgments

This work has been funded by the Spanish Ministerio de Economía y Competitividad (CGL2011–28681, CLG2010–21672, RYC–2009–04533 to D.M.A., and JCI–2010–08241 to I.C.–V.), the Generalitat de Catalunya (2009 SGR 754 GRC, and AGAUR's predoctoral grant FI–DGR 2012 to À.H.L.) and the University of Torino (Fondi ex–60% to M.D.). Fieldwork at ACM was funded by CESA Gestión de Residuos, S.A.U. We thank A. Martínez and Q. Soler for the temporary loan of extant specimens for comparison, the staff of the Preparation Division of the ICP for the preparation of the fossil specimens, B. Azanza and M. Rabi for providing several references, the reviewers J. Claude and M. Rabi for helpful comments that improved a previous version of this paper, and the following curators or researchers for permission to study fossil material under their care: F. Lapparent de Broin (MNHN, Paris); E. Jiménez (Sala de las Tortugas de la Universidad de Salamanca); Vicenç Vicedo (MGB, Barcelona); and S. Calzada (MGSB, Barcelona).

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